# HIERARCHIAL BEHAVIOR IN THE SOUTH AFRICAN CLAWED FROG, *Xenopus laevis* Daudin

By

ROBERT RICE HAUBRICH

A DISSERTATION PRESENTED TO THE GRADUATE COUNCIL OF
THE UNIVERSITY OF FLORIDA
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY

UNIVERSITY OF FLORIDA

August, 1957

ACKNOWLEDGMENTS

The writer wishes especially to acknowledge his indebtedness to the late Dr. W. C. Allee and his wife, Mrs. W. C. Allee (Ann Silver), whose ideas, encouragement and advice were instrumental in the production of this work. The close personal relationship with both of them remains one of his most cherished memories.

The writer also wishes to thank Dr. E. Ruffin Jones for taking on the burden of this program after the death of Dr. Allee, and wishes to acknowledge his indebtedness to him for encouragement and suggestions.

Gratitude also goes out to Dr. H. M. Wallbrunn who gave advice on statistics, Dr. C. J. Goin who suggested the experimental animal, Drs. L. Berner, J. H. Gregg, R. H. Waters and S. E. Wimberly who criticized the text and to many fellow students including C. D. Wilder, W. C. Sloan, C. D. Hynes, J. F. Howell and others for their discussions, criticisms and ideas relating to the development of this work.

TABLE OF CONTENT

## INTRODUCTION

Hierarchial behavior is a phenomenon in which individuals display certain aggressive actions toward one another such as pecking or nipping. Differences in the frequency of these actions are often consistent enough to enable one to rank individuals as to aggressive potential or position in relation to each other. Evidence of hierarchial behavior is found in such divergent parts of the animal kingdom as Arthropoda and Chordata.

Among invertebrates such behavior has been reported by Allee and Douglis (1945) in the hermit crab, Pagurus longicarpus, by Douglis (1946) in the lobster, Homarus americanus, by Pardii (1948) in the wasp, Polistes gallicus, by Bovjberg (1953) in the crayfish, Oronectes virilis and by Lowe (1956) in the crayfish, Cambarellus shufeldtii.

Among vertebrates evidence of hierarchial behavior is abundant in the class Osteichthyes. Braddock (1945) demonstrated it in Platypoecilus maculatus, as did Allee, Greenberg, Rosenthal and Frank (1948) in the green sunfish, Lepomis cyanellus. Newman's (1956) work gives information on intra- and interspecific competition as well as hierarchial behavior in two trout species, Salcelinus fontinalis (Mitchell) and Salmo gairdneri Richardson. Evidence of hierarchial behavior in the class Reptilia was reported by Greenberg and Noble (1944) in the American Chameleon, Anolis carolinensis.

Members of the class Aves probably have been studied with the greatest frequency and have yielded most in the way of facts and principles of hierarchial behavior. Papers by Schjelderup-Ebbe (1913, 1935) and Guhl

and Allee (1944) on the domestic fowl, Banks (1956) on jungle fowl, Diebschlag (1941) on pigeons, Bennett (1939) on ring doves, Howard and Emlen (1942) on quail, Hammerstrom (1942) on chickadees and Sabine (1949) on juncos and tree sparrows indicate the wide coverage in this class on both domesticated and wild forms.

Work on rats by Uhrich (1938), squirrels by Gordon (1940), infrahuman primates by Maslow (1940), chimpanzees by Crawford (1942) and Yerkes (1939), and the Rhesus monkey by Carpenter (1942) all demonstrate the social hierarchy in the class Mammalia. A form of hierarchial organization in human individual and group behavior is indicated by Haskins (1951), Allee (1951), Keith (1949), Sherif (1956) and others.

While this phenomenon reaches its greatest complexity among vertebrates (Allee, 1952) until recently no hierarchial behavior had been recorded for the classes Agnatha, Chondrichthyes or Amphibia. The first break in this situation occurred when Allee and Dickinson (1954) reported finding a primitive form of this behavior in the dogfish shark, Mustelus canis, a member of the class Chondrichthyes. This leaves Agnatha, regarded as the most primitive vertebrate class, and Amphibia, a class of medium complexity as the only two classes of Vertebrates in which there has been no report of hierarchial behavior.

Previous works have indicated aggression and territoriality in the class Amphibia, but not hierarchial behavior. Martof (1953) reported on a sort of territoriality observed among breeding males of the green frog, Rana clamitans, based on isolation, a type of intolerance, advertisement and fixation. He suggested that a relatively aggressive period is followed by

one of stability, which Collias (1944) considered to be the case in other vertebrates. Pearson (1955) found in the spadefoot toad, Scaphiopus holbrooki holbrooki (Harlan), avoidance reactions among individuals and a type of undefended home site territory which seldom overlapped others even in crowded areas. Test (1954) reported the first definite case of aggression in the class Amphibia as displayed in defense of territory by the frog, Phylobates trinitatis Boulenger. Evidence of territoriality in the bullfrog, Rana catesbeiana, was reported by O. B. Goin (1955). One frog was observed to croak and jump at a smaller frog in the same general area which resulted in the retreat of the smaller animal. In addition, other individuals were consistently found in certain areas located around a pool. Grant (1955) also reported on a case of territoriality in two species of salamanders, Eurycea bislineata and Hemidactylium scutatum, based upon a challenge and a defended territory, the means of defense included direct biting attack in E. bislineata and challenge only in H. scutatum.

Preliminary experiments were attempted on certain species of frogs but the problem of classifying the actions of the animals while under observation was difficult. Use of Xenopus laevis Daudin as the experimental animal was suggested by C. J. Goin (1953) of the University of Florida because of its habits and mode of life. The purpose of this study was fourfold: to determine whether hierarchial behavior was present in Xenopus, to analyze the phenomenon of hierarchial behavior, to fill a gap in reports of hierarchial behavior in different phylogenetic groups and to add to the information on aggression with possible applications to human behavior.

## EXPERIMENTAL

### Materials and Methods

Frogs used in this study were obtained from the supply house of Jay E. Cook, Cockneysville, Maryland and were received as adults by Cook from South Africa (see Walker, 1952). Prior to the observation period animals were kept in five gallon aquaria filled with water to a depth of ten inches. They were kept out of direct sunlight and temperatures were maintained between $60^{\circ}$ and $75^{\circ}$ F. The water was changed after each feeding or when it became cloudy. At first city water which had been conditioned by four days storage was used, but after some animals died local spring or stream water was used. The above methods for maintaining adults are discussed in detail by Parker, Robbins and Loveridge (1947).

Xenopus laevis was first described by Daudin (1803) and is primarily an aquatic frog. Adaptations to this aquatic habit are evident in the large webbed hind feet that permit rapid movement in any direction, a well-developed lateral line system (Elkan and Murray, 1951), ammonia excretion in adult (Munro, 1953), and nasal cavities lined with sensory epithelium that functions in olfactory perception when submerged (Paterson, 1951). In spite of the aquatic habit at times the animal is seen moving overland or is found in clods of mud near dried up ponds (Leslie, 1890; Rose, 1950).

Two groups of twelve female frogs each were used in this study and were kept in 8 - 10 inches of water at all times. Observations on frogs 1 - 12, designated as Experiment I or Group I took place in the Marine Biological Laboratory at Woods Hole from June to August 1954. Observations on

frogs 101 - 112, designated as Experiment II or Group II, were completed during the summer and fall of 1955 at the University of Florida.

Experiment I

Six frogs were kept between observations in each of two ten-gallon aquaria and were weighed once a week during the experimental period (Table 1). When animals were first received certain digits on the front limbs were clipped to facilitate recognition. Further clipping was unnecessary, even though digits grew back, because characteristics like size, color pattern, behavior and body shape varied widely among individuals and made it easy to recognize them after they had been observed for a time.

Pairs were observed separately in five-gallon aquaria. Before each series of pair observations water was changed and two different animals were used. During all observations cubes of liver, about 1/4 inch on a side, were placed in aquaria one at a time as the animals ate them. Feeding occurred only during time of observation.

Activity differences among individuals were noted by pairing frogs in all possible combinations. Each pair was observed a total of 200 minutes divided into ten twenty minute periods. These observation periods were conducted in two sets of five each. Periods within each set followed each other consecutively, excepting short breaks between periods for the experimenter to rest, but the two sets involving one pair of animals were not run consecutively. The following information was recorded during the pair observations for each frog:

1. Nips given. A nip was recorded when one frog nipped or bit another and caused the other to retreat.

2. Pushes given. A push was recorded when one frog approached another and displaced it through contact.

3. Approaches. Number of times each frog approached other motionless member of pair and touched without further activity.

4. Unknown. Number of times the two animals made contact, while in motion, with no observable differential between them.

5. Cubes of liver eaten by each frog and the order in which each was obtained.

6. The frog obtaining food first at the start of each series.

Activity differences were also noted when each frog was isolated a total of 200 minutes divided as in the paired situation into two series of ten twenty-minute periods each. The following information was recorded for each frog while isolated:

1. Number of cubes of liver eaten.

2. Time in seconds taken to obtain each piece of liver.

### Experiment II

In this experiment, in order to provide better control and prevent possible carryover of hierarchial behavior, the frogs were kept isolated in one gallon jars between observations. Paired and isolated animals were observed using methods similar to those in Experiment I. Temperatures varied between $71^{\circ}$ - $74^{\circ}$ F. and the animals were weighed weekly during pair observations (Table 1A). In Experiment II, to determine whether position in the hierarchy was consistent under different conditions, observations were made on each animal when in a group of twelve as well as when in a pair combination.

Since it was impossible to record the activities of all the frogs in the aquarium simultaneously the behavior of each frog with reference to the other eleven was observed for a total of 200 minutes. Each frog was under observation for a total of 200 minutes and only activities involving the single frog being observed at the moment were recorded. For instance, no record was kept of which animals were nipped by or received nips from the frog under observation. Observations were made like those on the paired situation, namely, in ten 20-minute periods at the rate of five periods a day. The animals were isolated a minimum of twelve hours after each daily observation.

## Results

Tables 1 and 1A indicate results of weekly weighings in number of grams. Individuals in Group I varied in average weights from 50 to 168 grams, while individuals in Group II varied from 37 to 140 grams. All of Group I (frogs 1 - 12) showed some gain during the experimental period as did all but three frogs in Group II (frogs 101 - 112).

When animals were placed together in pairs one of four different types of activity was observed, i. e. the nip, push, approach or unknown. These types of activity during contacts were recorded for each pairing and the results are shown in Tables 2 through 5.

Results in the nip category are recorded in Table 2 for frogs 1 - 12, and in Table 2A for frogs 101 - 112. Animals were ranked in order of total nips given in all pairings. In Experiment I this varied from 48 to 279, while in Experiment II it varied from 5 to 477. Ranking of frogs for total nips given (totals along the bottom row) was correlated to ranking for total

nips received (totals along the left column). Frogs 1 - 12 varied in total number of nips received from 76 to 254. When individual rankings in number of nips given were compared to rankings in number of nips received the results showed a correlation of -0.96. Frogs 101 - 112 varied in total number of nips received from 57 to 184, and when individual rankings in number of nips given were compared to rankings in nips received the result was a correlation of -0.50. A statistically significant difference at the 5 per cent level in number of nips given for any particular pairing is indicated in the tables by an asterisk following the greater value. In Table 2, 28 of the 66 pairings showed such a difference while in Table 2A, 34 of the 66 showed this difference.

Tables 3 and 3A are similar in form to the previous tables but deal with the push category. Individuals in Experiment I varied in total number of pushes given from 85 to 544 while those in Experiment II varied in this category from 20 to 377. Also, individuals in Group I varied in total pushes received from 103 to 381, while frogs in the other group varied from 71 to 262, When individual rankings in number of pushes given were compared to rankings in number of pushes received in Experiment I the result was a correlation of -0.87. In Experiment II when rankings were compared the result was a correlation of -0.76. In Table 3, 38 of the 66 pairings showed statistically significant differences between individuals in number of pushes given (shown by an asterisk following the larger total) while in Table 3A, 30 of the 66 pairings showed such differences.

Tables 4 and 4A deal with the approach category and are similar to those described above. Individuals in Experiment I varied in total number of

approaches made from 410 to 1248 while those in Experiment II varied in this category from 180 to 767. Individuals in Group I varied in the number of times each was approached from a minimum of 423 to a maximum of 1207, while animals in Group II varied from 277 to 773 in the same category. When individual rankings in number of approaches made were compared to rankings in approaches received in Experiment I the result was a correlation of -0.83, and in Experiment II the same comparisons produced a correlation of -0.88. In Table 4, 42 of the 66 pairings showed statistically significant differences, indicated by asterisks, between individuals in number of approaches made, while in Table 4A, 32 of the 66 pairings showed this.

The unknown category, represented by Tables 5 and 5A indicated the number of times frogs made contacts that were of equal or of no aggressive potential as nearly as the observer could determine. The numbers of contacts were the same for each member of each pair because both animals were given credit whenever a contact of this type occurred. The total number of contacts in the unknown category among individuals varied from 667 to 2525 in Experiment I and from 511 to 2411 in Experiment II.

In Tables 9 and 9A total food consumption, as measured by cubes of liver eaten, is recorded for each frog in each pair combination. The animals were ranked according to total number of cubes eaten over all pairings. Table 9 gives results for frogs 1 - 12 and shows an individual variation in food consumption from 151 to 327 units. Table 9A gives results for frogs 101 - 112 and the food consumption in this group varied from 75 to 803 units. When the rankings in total amount of food consumed by the other eleven frogs while paired with each frog were compared to rankings in total amount of

food eaten by each frog, correlations of -0.82 and -0.48 were recorded, respectively, in Experiments I and II. A statistically significant difference between frogs in amount of food eaten in any particular pairing was indicated in Tables 9 and 9A by an asterisk following the greater value. In Table 9, 19 out of the 66 pairings showed such a difference. In Table 9A, 26 out of the 66 pairings showed this difference.

Table 6 indicates number of nips and pushes that were given and received by each animal while in a group of twelve. A total of 313 nips were given by the 12 frogs during the observation period and individuals varied in total number of nips given from 0 to 168. A total of 193 nips were received by the 12 frogs during the period of observation, and individuals varied in the total number of nips received from 7 to 36. The total number of nips given by the group did not necessarily equal the total received because each frog was observed singly for 200 minutes and only nips given or received by that animal were recorded during this period. No record was kept of which frogs nipped or were nipped by the frog under observation. A negative correlation of 0.45 was found between total number of nips given among the 12 individuals and total nips received by these same individuals.

A total of 537 pushes were given by the group of 12 frogs and individuals varied from 5 to 136 in this category. A total of 735 pushes were received by all frogs and individuals varied from 19 to 142. The total number of pushes given did not equal the total number of pushes received for the reasons given above. A negative correlation of 0.62 was found between total number of pushes given among the 12 individuals and total pushes received by these same individuals. The total number of nips (given and

received) was 506 while the total number of pushes given and received was 1272.

Table 7 summarizes totals for the different behavioral categories from the paired situation. Frequencies of the categories increased consistently in both experiments from a minimum at the nip to a maximum at the unknown. Table 8, which summarizes frequencies of nips and pushes for groups of 12, also indicates an increase from nip to push (506 nips, 1272 pushes). Tables 7 and 8 indicate that an inverse relationship exists between frequency and aggressive intensity of contacts.

Comparisons in total amount of food consumed by frogs when isolated, paired and in groups of 12 are shown in Tables 10 and 10A. The total amount of food eaten by all frogs in 200 minutes increased from 441 units while isolated to 484 when paired to 1199 when in groups of 12. The latter figure is significantly larger than the other two values ($P = <0.01$ and $<0.05$, respectively).

The number of times each frog obtained food first at the start of a series of observations was recorded in Table 11. In the paired situation individuals varied from 4 to 16 in this category. When the group of twelve animals were compared a variation from 0 to 11 was observed.

Individual variation in average amount of time taken to obtain food while isolated was recorded in Table 12. The frogs in Experiment I varied from 72 to 768 seconds while those animals in Experiment II which ate varied from 54 to 1358 seconds, but two of the animals in Experiment II ate no food while isolated.

Table 13 shows rankings in each of the categories for frogs 1 - 12

These rankings to be used in correlation tests (Table 14) were obtained from the following tables:

| | |
|---|---|
| Nips while paired . . . . . . . . . . . . . . | Tables 2, 2A |
| Pushes while paired . . . . . . . . . . . . . | Tables 3, 3A |
| Approaches while paired . . . . . . . . . . . | Tables 4, 4A |
| Unknown while paired . . . . . . . . . . . . | Tables 5, 5A |
| Nips while in groups of twelve . . . . . . | Table 6 |
| Pushes while in groups of twelve . . . . . | Table 6 |
| Average weight . . . . . . . . . . . . . . . | Tables 1, 1A |
| Food consumption while in pairs . . . . . . | Tables 9, 9A |
| Time taken to locate food while isolated . | Table 12 |

Table 14 shows the correlation among all of the categories ranked in Table 13 for both sets of frogs. A measure of the statistical significance of these values also is indicated.

TABLE 1

WEIGHT, IN GRAMS, MEASURED DURING EXPERIMENTAL PERIOD
FROGS 1 - 12, EXPERIMENT I (1954)

| Date | Weight, in Grams, Frog Number | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
| 30 Jun | 131 | 170 | 105 | ... | 90 | 66 | .. | 66 | .. | 30 | 41 | 42 |
| 6 Jul | 128 | 168 | 117 | ... | 96 | 69 | .. | 70 | .. | 46 | 47 | 44 |
| 13 Jul | 127 | 172 | 109 | ... | 98 | 70 | .. | 67 | .. | 46 | 47 | 41 |
| 20 Jul | 127 | 259 | 104 | 128 | 95 | 68 | 72 | 72 | 53 | 46 | 50 | 50 |
| 27 Jul | 135 | 168 | 112 | 134 | 93 | 73 | 77 | 71 | 54 | 48 | 54 | 49 |
| 3 Aug | 136 | 172 | 107 | 137 | 97 | 69 | 77 | 67 | 54 | 50 | 55 | 51 |
| 10 Aug | 142 | 168 | 109 | 141 | 101 | 75 | 82 | 69 | 58 | 56 | 61 | 57 |
| 17 Aug | 141 | 167 | 113 | 144 | 104 | 78 | 85 | 72 | 61 | 58 | 69 | 64 |
| 24 Aug | 135 | 168 | 112 | 142 | 99 | 78 | 86 | 68 | 64 | 56 | 67 | 57 |
| 30 Aug | 142 | 174 | 112 | 137 | 103 | 76 | 84 | 70 | 67 | 63 | 70 | 60 |
| Av. Wt. | 134 | 168 | 110 | 138 | 98 | 72 | 80 | 69 | 59 | 50 | 56 | 52 |

TABLE 1A

WEIGHT, IN GRAMS, MEASURED DURING PAIR OBSERVATIONS
FROGS 101 - 112, EXPERIMENT II (1955)

| Date | Weight, in Grams, Frog Number | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 |
| 19 Jun | 105 | 96 | 132 | 84 | 74 | 64 | 65 | .. | 42 | 38 | .. | 32 |
| 26 Jun | 103 | 101 | 136 | 82 | 82 | 66 | 68 | .. | 43 | 41 | .. | 38 |
| 3 Jul | 101 | 106 | 133 | 83 | 77 | 60 | 68 | ... | 43 | 40 | .. | 37 |
| 10 Jul | 104 | 110 | 143 | 82 | 75 | 66 | 78 | .. | 43 | 39 | .. | 42 |
| 17 Jul | 101 | 108 | 139 | 93 | 77 | 68 | 78 | .. | 42 | 36 | .. | 43 |
| 24 Jul | 98 | 106 | 138 | 93 | 78 | 62 | 76 | .. | 44 | 39 | .. | 49 |
| 31 Jul | 102 | 110 | 138 | 90 | 75 | 62 | 82 | 79 | 49 | 36 | 55 | 51 |
| 7 Aug | 98 | 116 | 138 | 104 | 79 | 62 | 79 | 81 | 47 | 33 | .. | 48 |
| 14 Aug | 99 | 120 | 146 | 96 | 79 | 71 | 85 | 85 | 45 | 33 | .. | 54 |
| 7 Sep | 101 | 128 | 160 | 86 | 83 | 65 | 82 | 85 | 42 | 31 | 58 | 49 |
| Av. Wt. | 101 | 110 | 140 | 89 | 78 | 64 | 76 | 82 | 43 | 37 | 56 | 44 |

TABLE 2

TOTAL NIPS GIVEN BY FROGS IN PAIR COMBINATIONS
EXPERIMENT I[a]

| Frog No. | 1 | 4 | 2 | 6 | 5 | 12 | 11 | 7 | 10 | 9 | 8 | 3 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | .. | 17 | 14 | 10 | 5 | 5 | 4 | 5 | 5 | 4 | 4 | 3 | 76 |
| 4 | 19 | .. | 12 | 9 | 9 | 5 | 6 | 6 | 3 | 3 | 2 | 2 | 76 |
| 2 | 16 | 10 | .. | 20 | 5 | 3 | 4 | 5 | 5 | 8 | 5 | 5 | 86 |
| 6 | 25* | 12 | 17 | .. | 9 | 11 | 9 | 5 | 3 | 7 | 8 | 1 | 107 |
| 5 | 10 | 20 | 12 | 10 | .. | 9 | 4 | 7 | 3 | 6 | 1 | 9 | 91 |
| 12 | 41* | 15* | 7 | 9 | 18 | .. | 10 | 7 | 9 | 3 | 1 | 1 | 121 |
| 11 | 23* | 16* | 10 | 8 | 7 | 8 | .. | 9 | 7 | 2 | 7 | 2 | 99 |
| 7 | 16* | 22* | 18* | 21* | 15 | 6 | 9 | .. | 10 | 6 | 7 | 8 | 138 |
| 10 | 29* | 13* | 13 | 18 | 15 | 14 | 8 | 17 | .. | 4 | 9 | 3 | 143 |
| 9 | 26* | 19 | 17 | 16 | 21* | 21* | 22 | 5 | 11 | .. | 7 | 5 | 170 |
| 8 | 37* | 45* | 18 | 28* | 18* | 27* | 21* | 26* | 12 | 13 | .. | 9 | 254 |
| 3 | 37* | 32* | 35* | 22* | 5 | 11* | 15* | 11 | 11* | 10 | 2 | .. | 191 |
| Total[c] | 279 | 221 | 173 | 171 | 127 | 120 | 112 | 103 | 79 | 66 | 53 | 48 | 1552 |

a - Frogs numbered in each top row have nipped the frogs designated in each left column at the rate indicated in the Table. Columns indicate number of nips given by the frogs designated at top. Rows indicate number of nips received by frogs designated at left.
b - Column.
c - Row. Row-column rank correlation: Table 2 = -0.96
* - Significantly greater number of nips delivered (5 per cent level).

TABLE 2A

TOTAL NIPS GIVEN BY FROGS IN PAIR COMBINATIONS
EXPERIMENT II[a]

| Frog | 103 | 102 | 101 | 104 | 105 | 108 | 107 | 106 | 112 | 109 | 110 | 111 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 103 | ... | 15 | 7 | 18 | 3 | 2 | 9 | 2 | 0 | 1 | 0 | 0 | 57 |
| 102 | 29* | ... | 9 | 7 | 3 | 2 | 6 | 7 | 2 | 1 | 0 | 1 | 67 |
| 101 | 42 | 20 | ... | 8 | 8 | 8* | 10 | 11 | 7 | 1 | 1 | 0 | 116 |
| 104 | 20 | 26* | 13 | ... | 9 | 6 | 7 | 6 | 7 | 2 | 1 | 0 | 97 |
| 105 | 78* | 21* | 22 | 14 | ... | 6 | 11 | 12 | 15 | 2 | 3 | 0 | 184 |
| 108 | 43* | 30* | 2 | 0 | 3 | ... | 4 | 6 | 1 | 7 | 0 | 0 | 96 |
| 107 | 21 | 43* | 19 | 5 | 4 | 6 | ... | 2 | 3 | 3 | 0 | 0 | 106 |
| 106 | 76* | 28* | 10 | 12* | 7 | 15* | 15 | ... | 6 | 4 | 0 | 3 | 176 |
| 112 | 44* | 33* | 19 | 11 | 22 | 19* | 17* | 5 | ... | 1 | 0 | 1 | 172 |
| 109 | 44* | 53* | 21* | 13 | 11* | 9 | 7 | 2 | 5 | ... | 0 | 0 | 165 |
| 110 | 42* | 24* | 4 | 16* | 20 | 27* | 8* | 4* | 3 | 2 | ... | 0 | 150 |
| 111 | 38* | 34* | 0 | 0 | 14* | 1 | 4 | 5 | 1 | 0 | 1 | ... | 98 |
| Total[c] | 477 | 327 | 126 | 104 | 104 | 101 | 98 | 62 | 50 | 24 | 6 | 5 | 1484 |

a - Frogs numbered in each top row have nipped the frogs designated in each left column at the rate indicated in the Table. Columns indicate number of nips given by the frogs designated at top. Rows indicate number of nips received by frogs designated at left.

b - Column

c - Row. Row-column rank correlation: Table 2A = -0.50

* - Significantly greater number of nips delivered (5 per cent level).

TABLE 3

TOTAL PUSHES GIVEN BY FROGS IN PAIR COMBINATIONS
EXPERIMENT I[a]

| Frog | 1 | 4 | 2 | 11 | 5 | 6 | 12 | 3 | 7 | 8 | 9 | 10 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | .. | 28 | 30 | 5 | 3 | 5 | 5 | 7 | 6 | 7 | 5 | 2 | 104 |
| 4 | 32 | .. | 36 | 6 | 11 | 3 | 3 | 5 | 2 | 1 | 2 | 2 | 103 |
| 2 | 89* | 21 | .. | 3 | 17 | 11 | 9 | 7 | 3 | 6 | 1 | 3 | 170 |
| 11 | 46* | 20* | 30* | .. | 13 | 15 | 9 | 3 | 8 | 3 | 4 | 14 | 165 |
| 5 | 42* | 43* | 43* | 16 | .. | 13 | 0 | 37 | 7 | 7 | 3 | 1 | 212 |
| 6 | 45* | 35* | 39* | 13 | 9 | .. | 8 | 4 | 9 | 15 | 11 | 3 | 191 |
| 12 | 37* | 37* | 24* | 22 | 10 | 17 | .. | 1 | 11 | 14 | 4 | 10 | 187 |
| 3 | 37* | 77* | 79* | 43* | 27 | 26 | 17* | .. | 19 | 7 | 18 | 18 | 368 |
| 7 | 45* | 34* | 32* | 21* | 38* | 16 | 11 | 18 | .. | 10 | 14 | 2 | 241 |
| 8 | 72* | 84* | 37* | 34* | 25 | 23 | 40* | 9 | 21 | .. | 23* | 13 | 381 |
| 9 | 42* | 49* | 46* | 56* | 29* | 11 | 26* | 16 | 7 | 7 | .. | 17 | 306 |
| 10 | 57* | 59* | 34* | 18 | 27 | 14 | 20 | 8 | 11 | 12 | 3 | .. | 263 |
| Total[c] | 544 | 487 | 430 | 237 | 209 | 154 | 148 | 115 | 104 | 90 | 88 | 85 | 2691 |

a - Frogs numbered in each top row have pushed the frogs designated in each left column at the rate indicated in the Table. Columns indicate number of pushes given by the frogs designated at top. Rows indicate number of pushes received by frogs designated at left.

b - Column.

c - Row. Row-column rank correlation: Table 3 = -0.87

* - Significantly greater number of pushes delivered (5 per cent level).

TABLE 3A

TOTAL PUSHES GIVEN BY FROGS IN PAIR COMBINATIONS
EXPERIMENT II[a]

| Frog | 103 | 102 | 107 | 108 | 101 | 106 | 105 | 104 | 112 | 111 | 109 | 110 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 103 | ... | 11 | 16 | 3 | 12 | 5 | 2 | 18 | 2 | 1 | 1 | 0 | 71 |
| 102 | 21 | ... | 10 | 1 | 11 | 6 | 5 | 13 | 2 | 1 | 4 | 0 | 74 |
| 107 | 13 | 43* | ... | 17 | 16 | 2 | 8 | 7 | 1 | 4 | 5 | 1 | 117 |
| 108 | 37* | 39* | 18 | ... | 7 | 17 | 9 | 0 | 1 | 1 | 3 | 0 | 132 |
| 101 | 34 | 17 | 28 | 37* | ... | 22 | 15 | 20 | 6 | 1 | 3 | 0 | 183 |
| 106 | 56* | 18* | 38 | 17 | 8 | ... | 19 | 21 | 4 | 1 | 3 | 3 | 188 |
| 105 | 44* | 34 | 32* | 5 | 35 | 19 | ... | 10 | 24 | 2 | 0 | 1 | 206 |
| 104 | 11 | 14 | 25 | 20 | 14 | 15 | 11 | ... | 2 | 1 | 4 | 0 | 117 |
| 112 | 43* | 11* | 39* | 35* | 17* | 21* | 16 | 4 | ... | 15 | 4 | 2 | 207 |
| 111 | 35* | 37* | 10 | 8* | 10* | 19* | 14* | 1 | 4 | ... | 7 | 4 | 149 |
| 109 | 33* | 55* | 16* | 13* | 23* | 4 | 7* | 14 | 6 | 4 | ... | 9 | 184 |
| 110 | 50* | 23* | 22* | 66* | 27* | 13* | 21* | 11* | 7 | 13 | 9 | ... | 262 |
| Totals[c] | 377 | 302 | 254 | 222 | 180 | 143 | 127 | 119 | 59 | 44 | 43 | 20 | 1890 |

a - Frogs numbered in each top row have pushed the frogs designated in each left column at the rate indicated in the Table. Columns indicate number of pushes given by the frogs designated at top. Rows indicate number of pushes received by frogs designated at left.

b - Columns.

c - Rows. Row-column rank correlation: Table 3A = -0.76

* - Significantly greater number of pushes delivered (5 per cent level).

TABLE 4

TOTAL APPROACHES GIVEN BY FROGS IN PAIR COMBINATIONS
EXPERIMENT I[a]

| Frog | 1 | 2 | 5 | 4 | 6 | 11 | 12 | 10 | 7 | 8 | 9 | 3 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ... | 76 | 63 | 58 | 55 | 56 | 37 | 39 | 32 | 58 | 37 | 58 | 569 |
| 2 | 115* | ... | 81 | 79 | 77 | 37 | 51 | 46 | 52 | 45 | 48 | 58 | 689 |
| 5 | 136* | 72 | ... | 79* | 101 | 60 | 24 | 20 | 27 | 67 | 38 | 56 | 680 |
| 4 | 86* | 77 | 35 | ... | 37 | 42 | 21 | 31 | 22 | 22 | 17 | 33 | 423 |
| 6 | 86 | 91 | 101 | 67 | ... | 59 | 51 | 41 | 33 | 57 | 35 | 26 | 647 |
| 11 | 91* | 63* | 51 | 48 | 70 | ... | 74 | 77 | 29 | 27 | 24 | 11 | 565 |
| 12 | 33* | 62 | 83* | 65* | 93 | 89 | ... | 84 | 57 | 45 | 25 | 24 | 760 |
| 10 | 97* | 68 | 104* | 73* | 75* | 63 | 111 | ... | 55 | 51 | 36 | 19 | 752 |
| 7 | 103* | 80 | 106* | 78* | 93* | 65* | 52 | 45 | ... | 41 | 35 | 36 | 734 |
| 8 | 161* | 136* | 128* | 140* | 132* | 89* | 133* | 54 | 109* | ... | 58* | 50 | 1190 |
| 9 | 67* | 118* | 108* | 93* | 21 | 122* | 108* | 83 | 28 | 30 | ... | 39 | 817 |
| 3 | 173* | 173* | 88 | 142* | 116* | 133* | 80* | 97* | 73* | 33 | 99* | ... | 1207 |
| Total[c] | 1248 | 1016 | 948 | 922 | 870 | 815 | 742 | 617 | 517 | 476 | 452 | 410 | 9033 |

a- Frogs numbered in each top row have approached the frogs designated in each left column at the rate indicated in the Table. Columns indicate number of approaches given by the frogs designated at top. Rows indicate number of approaches received by frogs designated at left.
b- Columns.
c- Rows. Row-column rank correlation: Table 4 = -0.83
*- Significantly greater number of approaches (5 per cent level).

TABLE 4A

TOTAL APPROACHES GIVEN BY FROGS IN PAIR COMBINATIONS

EXPERIMENT II[a]

| Frog | 107 | 102 | 103 | 108 | 106 | 101 | 105 | 104 | 109 | 112 | 111 | 110 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 107 | ... | 91* | 30 | 34 | 41 | 20 | 19 | 10 | 19 | 19 | 21 | 7 | 311 |
| 102 | 48 | ... | 41 | 15 | 35 | 28 | 25 | 25 | 15 | 20 | 16 | 9 | 277 |
| 103 | 75 | 35 | ... | 17 | 21 | 56 | 11 | 67* | 16 | 15 | 15 | 14 | 342 |
| 108 | 40 | 64* | 60 | ... | 47 | 14 | 27 | 1 | 11 | 7 | 14 | 9 | 294 |
| 106 | 84 | 56 | 43 | 36 | ... | 18 | 37 | 49 | 32 | 16 | 13 | 6 | 390 |
| 101 | 73* | 54 | 49 | 83* | 50* | ... | 40 | 28 | 21 | 32 | 14 | 13 | 457 |
| 105 | 51* | 62* | 101* | 14 | 79 | 51 | ... | 48 | 40 | 36 | 14 | 26 | 522 |
| 104 | 74* | 29 | 28 | 47* | 50 | 32 | 43 | ... | 37 | 18 | 10 | 26 | 394 |
| 109 | 47* | 84* | 79* | 45* | 37 | 50* | 32 | 51 | ... | 18 | 9 | 18 | 470 |
| 112 | 89* | 57* | 92* | 91* | 47* | 35 | 32 | 27 | 21 | ... | 37 | 21 | 549 |
| 111 | 66* | 95* | 57* | 39 | 31 | 29* | 65* | 7 | 12 | 28 | ... | 31 | 460 |
| 110 | 120* | 97* | 99* | 109* | 70* | 74* | 59 | 44 | 39 | 16 | 46 | ... | 773 |
| Total[c] | 767 | 724 | 679 | 530 | 508 | 407 | 390 | 357 | 213 | 225 | 209 | 180 | 5239 |

a - Frogs numbered in each top row have approached the frogs designated in each left column at the rate indicated in the Table. Columns indicate number of approaches given by the frogs designated at top. Rows indicate number of approaches received by frogs designated at left.

b - Columns.

c - Rows. Row-column rank correlation: Table 4A = -0.88

* - Significantly greater number of approaches (5 per cent level).

TABLE 5

TOTAL CONTACTS SHOWING NO OBSERVED AGGRESSIVE DIFFERENCES
BETWEEN FROGS WHILE IN PAIRS (UNKNOWN CATEGORY)
EXPERIMENT I

| Frog | 4 | 11 | 5 | 7 | 6 | 9 | 2 | 10 | 12 | 1 | 8 | 3 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 | ... | 314 | 317 | 331 | 224 | 186 | 262 | 224 | 263 | 209 | 128 | 67 | 2525 |
| 11 | 314 | ... | 338 | 255 | 236 | 146 | 154 | 177 | 130 | 265 | 176 | 70 | 2261 |
| 5 | 317 | 338 | ... | 185 | 251 | 322 | 167 | 253 | 175 | 139 | 106 | 0 | 2253 |
| 7 | 331 | 255 | 185 | ... | 157 | 101 | 257 | 248 | 229 | 267 | 155 | 115 | 2200 |
| 6 | 224 | 236 | 251 | 157 | ... | 253 | 221 | 129 | 233 | 161 | 121 | 56 | 2042 |
| 9 | 186 | 146 | 322 | 101 | 253 | ... | 234 | 116 | 156 | 188 | 127 | 100 | 1929 |
| 2 | 262 | 154 | 167 | 257 | 221 | 234 | ... | 193 | 195 | 0 | 160 | 63 | 1906 |
| 10 | 224 | 177 | 253 | 248 | 129 | 116 | 193 | ... | 156 | 203 | 106 | 55 | 1860 |
| 12 | 263 | 130 | 175 | 229 | 233 | 156 | 195 | 156 | ... | 204 | 0 | 60 | 1801 |
| 1 | 209 | 265 | 139 | 167 | 161 | 188 | 0 | 203 | 204 | ... | 74 | 61 | 1671 |
| 8 | 128 | 176 | 106 | 155 | 121 | 127 | 160 | 106 | 0 | 74 | ... | 20 | 1173 |
| 3 | 67 | 70 | 0 | 115 | 56 | 100 | 63 | 55 | 60 | 61 | 20 | ... | 667 |
| Total | 2525 | 2261 | 2253 | 2200 | 2042 | 1929 | 1906 | 1860 | 1801 | 1671 | 1173 | 667 | 22288 |

TABLE 5A

TOTAL CONTACTS SHOWING NO OBSERVED AGGRESSIVE DIFFERENCES BETWEEN FROGS WHILE IN PAIRS (UNKNOWN CATEGORY)
EXPERIMENT II

| Frog | 102 | 106 | 103 | 107 | 108 | 104 | 105 | 109 | 112 | 101 | 110 | 111 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 102 | ... | 328 | 240 | 223 | 314 | 450 | 262 | 93 | 197 | 122 | 84 | 98 | 2411 |
| 106 | 328 | ... | 192 | 210 | 335 | 304 | 235 | 198 | 131 | 85 | 29 | 35 | 2082 |
| 103 | 240 | 192 | ... | 197 | 272 | 273 | 225 | 136 | 131 | 115 | 64 | 138 | 1983 |
| 107 | 223 | 210 | 197 | ... | 261 | 224 | 227 | 209 | 212 | 71 | 59 | 70 | 1963 |
| 108 | 314 | 335 | 272 | 261 | ... | 44 | 166 | 199 | 130 | 141 | 61 | 22 | 1945 |
| 104 | 450 | 304 | 273 | 224 | 44 | ... | 126 | 168 | 71 | 177 | 64 | 3 | 1904 |
| 105 | 262 | 235 | 225 | 227 | 166 | 126 | ... | 137 | 89 | 153 | 53 | 65 | 1738 |
| 109 | 93 | 198 | 136 | 209 | 199 | 168 | 137 | ... | 133 | 115 | 32 | 12 | 1432 |
| 112 | 197 | 131 | 131 | 212 | 130 | 71 | 89 | 133 | ... | 137 | 24 | 22 | 1277 |
| 101 | 122 | 85 | 115 | 71 | 141 | 177 | 153 | 115 | 137 | ... | 88 | 21 | 1225 |
| 110 | 84 | 29 | 64 | 59 | 61 | 64 | 53 | 32 | 24 | 88 | ... | 25 | 583 |
| 111 | 98 | 35 | 138 | 70 | 22 | 3 | 65 | 12 | 22 | 21 | 25 | ... | 511 |
| Total | 2411 | 2082 | 1983 | 1963 | 1945 | 1904 | 1738 | 1432 | 1277 | 1225 | 583 | 511 | 19054 |

TABLE 6

NUMBER OF NIPS AND PUSHES GIVEN AND RECEIVED BY EACH FROG WHEN PRESENT IN AN AQUARIUM WITH ELEVEN OTHER ANIMALS - EXPERIMENT II

| Frog | Nips Given | Nips Received | Pushes Given | Pushes Received | Nips-Pushes Given | Nips-Pushes Received |
|---|---|---|---|---|---|---|
| 101 | 19 | 13 | 39 | 33 | 58 | 46 |
| 102 | 64 | 12 | 130 | 28 | 194 | 40 |
| 103 | 168 | 7 | 136 | 26 | 304 | 33 |
| 104 | 17 | 19 | 60 | 35 | 77 | 54 |
| 105 | 9 | 8 | 25 | 53 | 34 | 61 |
| 106 | 14 | 19 | 32 | 44 | 46 | 63 |
| 107 | 10 | 13 | 53 | 38 | 63 | 51 |
| 108 | 0 | 14 | 6 | 89 | 6 | 103 |
| 109 | 0 | 33 | 5 | 142 | 5 | 175 |
| 110 | 2 | 36 | 10 | 134 | 12 | 170 |
| 111 | 2 | 14 | 28 | 94 | 30 | 108 |
| 112 | 8 | 5 | 13 | 19 | 21 | 24 |
| Total | 313* | 193* | 537* | 735* | 850 | 928 |

* - Total nips or pushes given in this case do not necessarily equal total nips or pushes received because in the grouped situation frogs were observed one at a time. No record was kept of which frogs gave nips or pushes to or received nips or pushes from the particular animal being observed.

Correlation ($r_{xy}$) between number of nips given and nips received was -0.45

Correlation ($r_{xy}$) between number of pushes given and pushes received was -0.62

TABLE 7

FREQUENCY OF EACH CONTACT TYPE WHEN FROGS WERE IN PAIRS

| Type of Contact | Number Observed Experiment | | Per Cent of Total Experiment | |
|---|---|---|---|---|
| | I | II | I | II |
| Nip | 1552 | 1484 | 6.4 | 8.2 |
| Push | 2691 | 1890 | 11.0 | 10.4 |
| Approach | 9033 | 5239 | 37.0 | 28.9 |
| Unknown | 11144 | 9527 | 45.6 | 52.5 |
| Total | 24420 | 18140 | 100.0 | 100.0 |

TABLE 8

FREQUENCY OF EACH CONTACT TYPE WHEN FROGS WERE IN GROUP OF TWELVE

| Type of Contact | Number Observed |
|---|---|
| Nip | 506 |
| Push | 1272 |
| Total | 1778 |

TABLE 9

UNITS OF FOOD CONSUMED BY EACH FROG IN EACH PAIR COMBINATION[a]

| Frog | 4 | 1 | 11 | 10 | 5 | 7 | 12 | 2 | 6 | 9 | 8 | 3 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 4 | .. | 33 | 25 | 15 | 27 | 21 | 21 | 26 | 11 | 17 | 13 | 9 | 218 |
| 1 | 14 | .. | 26 | 25 | 12 | 24 | 16 | 12 | 16 | 13 | 8 | 9 | 175 |
| 11 | 25 | 24 | .. | 14 | 32 | 21 | 14 | 20 | 19 | 8 | 24 | 12 | 213 |
| 10 | 35* | 25 | 26 | .. | 26 | 24 | 25 | 17 | 20 | 17 | 10 | 15 | 240 |
| 5 | 23 | 30* | 18 | 23 | .. | 20 | 21 | 23 | 20 | 14 | 14 | 22* | 228 |
| 7 | 29 | 26 | 26 | 27 | 30 | .. | 26 | 30 | 19 | 14 | 22 | 21 | 270 |
| 12 | 27 | 34* | 17 | 15 | 26 | 24 | .. | 17 | 26 | 17 | 8 | 9 | 220 |
| 2 | 24 | 15 | 30 | 33 | 27 | 20 | 33 | .. | 28 | 14 | 25 | 13 | 262 |
| 6 | 39* | 34* | 30 | 19 | 20 | 32 | 21 | 21 | .. | 29 | 21 | 14 | 280 |
| 9 | 33 | 37* | 42* | 33* | 36 | 23 | 31 | 36 | 17 | .. | 24 | 18 | 330 |
| 8 | 37* | 22 | 26 | 37* | 28 | 28 | 19 | 25 | 18 | 20 | .. | 9 | 269 |
| 3 | 41* | 29* | 35* | 31* | 3 | 29 | 31* | 28* | 31* | 30 | 17 | .. | 305 |
| Total[c] | 327 | 309 | 301 | 272 | 267 | 266 | 258 | 255 | 225 | 193 | 186 | 151 | 3010 |

a - Frogs numbered in the rows along the top of the Table have eaten the number of food units shown while in the presence of the frogs designated in the left column of the Table.

b - Column.

c - Row. Row-column rank correlation: Table 9 = -0.82

* - Significantly greater amount of food eaten (5 per cent level).

TABLE 9A

UNITS OF FOOD CONSUMED BY EACH FROG IN EACH PAIR COMBINATION[a]

| Frog | 102 | 103 | 107 | 108 | 105 | 104 | 101 | 112 | 106 | 109 | 110 | 111 | Total[b] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 102 | ... | 51 | 23 | 42 | 33 | 54 | 26 | 41 | 37 | 20 | 8 | 13 | 348 |
| 103 | 62 | ... | 79 | 61 | 38 | 83* | 51 | 36 | 12 | 14 | 3 | 3 | 442 |
| 107 | 83* | 55 | ... | 83* | 30 | 31 | 23 | 40 | 23 | 57 | 12 | 8 | 445 |
| 108 | 81* | 84 | 40 | ... | 44 | 0 | 16 | 20 | 35 | 49 | 9 | 7 | 385 |
| 105 | 62 | 88* | 72* | 41 | ... | 33 | 63 | 44 | 29 | 27 | 18 | 5 | 482 |
| 104 | 64 | 30 | 78 | 68* | 40 | ... | 37 | 37 | 41 | 38 | 13 | 0 | 446 |
| 101 | 52 | 43 | 41 | 56* | 29 | 40 | ... | 36 | 53 | 36 | 17 | 5 | 408 |
| 112 | 62 | 72 | 68 | 74* | 30 | 36 | 22 | ... | 19 | 12 | 9 | 14 | 418 |
| 106 | 77* | 72 | 80* | 85* | 52 | 78* | 17 | 32 | ... | 33 | 5 | 13 | 544 |
| 109 | 94* | 71* | 69 | 67 | 32 | 18 | 43 | 45* | 21 | ... | 11 | 4 | 475 |
| 110 | 70* | 77* | 60* | 60* | 39 | 25 | 35 | 11 | 13 | 15 | ... | 3 | 408 |
| 111 | 96* | 98* | 91* | 40* | 67* | 1 | 22* | 9 | 54 | 12 | 13 | ... | 503 |
| Total[c] | 803 | 741 | 701 | 677 | 434 | 399 | 355 | 351 | 337 | 313 | 118 | 75 | 5304 |

a - Frogs numbered in the rows along the top of the Table have eaten the number of food units shown while in the presence of the frogs designated in the left column of the Table.

b - Column.

c - Row. Row-column rank correlation: Table 9A = -0.48

* - Significantly greater amount of food eaten (5 per cent level).

TABLE 10

TOTAL UNITS OF FOOD EATEN BY FROGS DURING OBSERVATION TIME OF 200 MINUTES WHEN ISOLATED, PAIRED* AND IN GROUP OF TWELVE EXPERIMENT II

| Frog | Total Units Eaten | | |
| --- | --- | --- | --- |
| | Isolated | Paired* | Grouped |
| 101 | 56 | 32 | 106 |
| 102 | 50 | 73 | 167 |
| 103 | 113 | 68 | 157 |
| 104 | 0 | 36 | 191 |
| 105 | 55 | 39 | 81 |
| 106 | 50 | 31 | 98 |
| 107 | 69 | 64 | 110 |
| 108 | 0 | 62 | 19 |
| 109 | 25 | 28 | 41 |
| 110 | 5 | 12 | 21 |
| 111 | 12 | 7 | 68 |
| 112 | 6 | 32 | 140 |
| Total | 441 | 484 | 1199 |

* - Average value of 200 minutes taken from total observation time of 2400 minutes for each frog.

TABLE 10A

STATISTICAL TEST OF DIFFERENCES AMONG THE ISOLATED, PAIRED AND GROUPED SITUATIONS CONSIDERED IN TABLE 10

| Comparison | t | P< |
| --- | --- | --- |
| Isolated-Paired | 0.42 | 0.7 |
| Isolated-Grouped | 3.97 | 0.01 |
| Paired-Grouped | 2.69 | 0.05 |

TABLE 11

NUMBER OF TIMES EACH FROG OBTAINED FOOD FIRST WHILE MEMBER OF A PAIR - EXPERIMENTS I AND II - AND WHILE IN A GROUP OF TWELVE EXPERIMENT II

| Paired | | | | Grouped |
|---|---|---|---|---|
| Frog | Times | Frog | Times | Times |
| 1 | 15 | 101 | 10 | 6 |
| 2 | 8 | 102 | 13 | 4 |
| 3 | 6 | 103 | 9 | 3 |
| 4 | 15 | 104 | 8 | 7 |
| 5 | 11 | 105 | 11 | 6 |
| 6 | 12 | 106 | 10 | 3 |
| 7 | 11 | 107 | 17 | 0 |
| 8 | 10 | 108 | 14 | 1 |
| 9 | 4 | 109 | 15 | 0 |
| 10 | 16 | 110 | 6 | 2 |
| 11 | 12 | 111 | 3 | 2 |
| 12 | 12 | 112 | 14 | 11 |
| Total | 132 | | 130 | 45 |

TABLE 12

AVERAGE NUMBER OF SECONDS TAKEN BY FROGS WHEN ISOLATED TO OBTAIN EACH UNIT OF FOOD - EXPERIMENTS I AND II

| Frog | Average Time | Frog | Average Time |
|---|---|---|---|
| 1 | 82 | 101 | 114 |
| 2 | 72 | 102 | 132 |
| 3 | 768 | 103 | 54 |
| 4 | 62 | 104 | ... |
| 5 | 74 | 105 | 824 |
| 6 | 157 | 106 | 1358 |
| 7 | 169 | 107 | 76 |
| 8 | 220 | 108 | ... |
| 9 | 137 | 109 | 256 |
| 10 | 130 | 110 | 299 |
| 11 | 83 | 111 | 342 |
| 12 | 118 | 112 | 389 |

TABLE 13

RANKINGS OF FROGS IN VARIOUS CATEGORIES
EXPERIMENTS I AND II

| Frog | Nip | Push | Approach | Unknown | Grouped Nip | Grouped Push | Food Eaten | Food Time | Weight |
|---|---|---|---|---|---|---|---|---|---|
| EXPERIMENT I | | | | | | | | | |
| 1 | 1 | 1 | 1 | 10 | .. | .. | 2 | 4 | 3 |
| 2 | 3 | 3 | 2 | 7 | .. | .. | 8 | 2 | 1 |
| 3 | 12 | 8 | 12 | 12 | .. | .. | 12 | 12 | 4 |
| 4 | 2 | 2 | 4 | 1 | .. | .. | 1 | 1 | 2 |
| 5 | 5 | 5 | 3 | 3 | .. | .. | 5 | 3 | 5 |
| 6 | 4 | 6 | 5 | 5 | .. | .. | 9 | 9 | 7 |
| 7 | 8 | 9 | 9 | 4 | .. | .. | 6 | 10 | 6 |
| 8 | 11 | 10 | 10 | 11 | .. | .. | 11 | 11 | 8 |
| 9 | 10 | 11 | 11 | 6 | .. | .. | 10 | 8 | 9 |
| 10 | 9 | 12 | 8 | 8 | .. | .. | 4 | 7 | 12 |
| 11 | 7 | 4 | 6 | 2 | .. | .. | 3 | 5 | 10 |
| 12 | 6 | 7 | 7 | 9 | .. | .. | 7 | 6 | 11 |
| EXPERIMENT II | | | | | | | | | |
| 101 | 3 | 5 | 6 | 10 | 3 | 5 | 7 | 3 | 3 |
| 102 | 2 | 2 | 2 | 1 | 2 | 2 | 1 | 4 | 2 |
| 103 | 1 | 1 | 3 | 3 | 1 | 1 | 2 | 1 | 1 |
| 104 | 4 | 8 | 8 | 6 | 4 | 3 | 6 | 11 | 4 |
| 105 | 5 | 7 | 7 | 7 | 7 | 7 | 5 | 9 | 6 |
| 106 | 8 | 6 | 5 | 2 | 5 | 6 | 9 | 10 | 5 |
| 107 | 7 | 3 | 1 | 4 | 6 | 4 | 3 | 2 | 7 |
| 108 | 6 | 4 | 4 | 5 | 11 | 11 | 4 | 12 | 8 |
| 109 | 10 | 11 | 9 | 8 | 12 | 12 | 10 | 5 | 11 |
| 110 | 11 | 12 | 12 | 11 | 10 | 10 | 11 | 6 | 12 |
| 111 | 12 | 10 | 11 | 12 | 9 | 8 | 12 | 7 | 9 |
| 112 | 9 | 9 | 10 | 9 | 8 | 9 | 8 | 8 | 10 |

TABLE 14

RANK CORRELATIONS OF THE CATEGORIES WITH TESTS INDICATING PROBABILITY OF CORRELATION BEING AS LARGE OR LARGER DUE TO CHANCE ALONE (Edwards, 1954)

| Comparisons | Frogs 1 - 12 | | Frogs 101 - 112 | |
|---|---|---|---|---|
| | Correlation | P < | Correlation | P < |
| Nip/Push | 0.85 | 0.01 | 0.81 | 0.01 |
| Nip/Approach | .94 | .01 | .70 | .01 |
| Push/Approach | .84 | .01 | .94 | .01 |
| Nip/Unknown | .40 | .2 | .61 | .05 |
| Push/Unknown | .32 | .3 | .77 | .01 |
| Approach/Unknown | .35 | .3 | .85 | .01 |
| Paired Grouped | | | | |
| Nip Nip | .... | .... | .81 | .01 |
| Push Push | .... | .... | .71 | .01 |
| Nip Push | .... | .... | .76 | .01 |
| Grouped Nip/Grouped Push | .... | .... | .97 | .01 |
| Nip/Food Consumption | .66 | .02 | .85 | .01 |
| Push/Food Consumption | .55 | .1 | .90 | .01 |
| Approach/Food Consumption | .64 | .05 | .87 | .01 |
| Unknown/Food Consumption | .56 | .1 | .76 | .01 |
| Nip/Food Time | .82 | .01 | .27 | .4 |
| Push/Food Time | .73 | .01 | .36 | .3 |
| Approach/Food Time | .83 | .01 | .36 | .3 |
| Unknown/Food Time | .52 | .1 | .06 | .9 |
| Nip/Weight | .52 | .1 | .91 | .01 |
| Push/Weight | .67 | .02 | .80 | .01 |
| Approach/Weight | .49 | .1 | .80 | .01 |
| Unknown/Weight | .08 | .8 | .63 | .05 |
| Food Consumption/Food Time | .73 | .01 | .26 | .5 |
| Food Consumption/Weight | .10 | .8 | .70 | .01 |
| Food Time/Weight | .38 | .3 | .28 | .5 |

## DISCUSSION OF RESULTS

This study is concerned with three basic problems all dealing with hierarchial behavior: the behavioral display of aggression in frogs, individual differences as to aggressive behavior and factors related to individual differences in aggression.

The statistically significant correlations that are seen in Table 14 when rankings of frogs in the nip, push and approach categories are compared support the assumption that these three categories represent different expressions of the same thing, namely, aggression. In addition, the hierarchial standing of frogs 101 - 112 in the nip and push categories as indicated from pairings are highly correlated with hierarchial positions of the same frogs when observed in a group of twelve (Tables 6 and 14). Thus, frogs nipping the most also push most whether they are observed in successive pairs or as members of a group of twelve.

Correlations between rankings in the unknown and aggressive categories are generally much lower than correlations among rankings in each of the aggressive categories (Table 14). This is evidence that the unknown category is different and while it may include aggressive activity of a low level, it also includes activities of a non-aggressive nature.

Table 7 shows the frequencies of the nip, push, approach and unknown categories when frogs were paired. The unknown category makes up about 50 per cent of all contacts, somewhat over 30 per cent of all contacts show a weak form of aggression referred to as the approach, a little more than 10 per cent show definite aggression in the push and somewhat less than 10 per

cent indicate the most intense form of aggression, namely, the nip. Tables 6 and 8 give frequencies of the nip and push categories when frogs were in a group of twelve. The relative frequencies of nips and pushes are of the same order whether animals are paired or in a group of twelve. A negative relationship exists between intensity of aggression and its frequency of expression whether frogs are observed in a series of pairings or in a group of twelve.

Each group of frogs displayed a rather loose form of hierarchy based upon differences among individuals in aggressive potential as measured by the nip, push and approach. Tables 2 - 5 show the structure, arrangement and extend of these individual differences. Wide variations among frogs are indicated when all aggressive activity is totaled for each animal. Differences in aggressive activity between individuals in any one pair are noted by comparing totals for each grog within the chart. Fifty per cent of the differences between members of pairs are statistically significant as indicated by asterisks in the squares of the greater totals. The per cent of significantly different totals remains consistent for both groups of frogs tested and also for the three aggressive categories.

Rank correlation between total aggressive activity expressed and total aggressive activity permitted in this study is negative and statistically significant. Frogs with the highest aggressive potential, as measured by number of nips, pushes and approaches administered, experience the fewest aggressive advances from other frogs and vice versa. This suggests that aggression is a distinct form of behavior and is based upon certain behavioral cues not detected by the observer.

Other information recorded during periods of observations included the following: (1) weights, (2) amounts of food eaten and comparisons when frogs were isolated, paired and grouped, (3) time taken to obtain food while isolated and (4) number of times food was obtained first when individuals were in pairs or in a group of twelve.

Table 14 shows correlations between all of the factors. It is from these correlations, based upon rankings of the frogs (Table 13), that most interpretations regarding relationships are made.

Weight differences might be thought of as one expression of physiological variation. When rankings in weight, obtained from Table 1, are correlated with rankings in the nip, push, approach and unknown categories the results are variable (Table 14). Differences noted previously between aggressive behavior and the unknown category carry through when the weight factor is considered. Four of the six correlations between the aggressive categories and weight are statistically significant and the other two are almost so. All are positive. Weight is considered to be a factor in hierarchial behavior of these frogs and heavier frogs tend to rank higher in the three aggressive categories, namely, nip, push and approach, yet do not necessarily rank higher in the unknown category.

Tables 9 and 9A show how frogs rank in individual food consumption. Differences in food consumption are not as clear-cut as those within each of the aggressive categories. Less than 50 per cent of the pairings show significant differences between frogs as indicated by asterisks within the tables. Also, when rankings of frogs in total food consumed (totals in bottom row) are compared to rankings in total food consumed by others in

their presence (totals in right column) the results are inconclusive. Group I shows a significantly high correlation, Group II does not, although, all correlations are negative.

When rankings in weight are compared to rankings in amount of food eaten the results are variable. The heaviest animals in Group II tend to eat the most whereas the heaviest in Group I do not necessarily eat the most. When rankings in food consumption are correlated with those in the three aggressive categories and the unknown the results are statistically significant at the 5 per cent level in six out of eight cases and close in the remaining two. There is no break in degree of correlation observed here, as in previous comparisons, between the three aggressive categories and the unknown, which indicates the more aggressive as well as the more active frogs eat more than the less aggressive and less active animals.

The average time taken by isolated animals to locate food varies widely among individuals (Table 12). These differences may be due to variations in the chemoreceptor systems and in ability to respond to these stimuli. When rankings in this category are compared to rankings in the aggressive categories (Table 14) the correlations, while all positive and significant at the 5 per cent level in Group I, are positive but of questionable significance in Group II. When rankings in amount of time taken to locate food are compared to rankings in amount of food consumed the correlations are not consistently high. Therefore, the more aggressive frogs do not necessarily find food more quickly, nor do the frogs eating more while paired necessarily take the least time to locate food when isolated.

Information on the number of times each frog obtained food first while a member of a pair and while in a group of twelve is given in Table 11. Which animal obtains food first at the start of each series of observations is apparently a chance phenomenon not noticeably related to any factors previously discussed.

It is possible that the three aggressive categories represent attempts by frogs to eat one another. Cannibalism is well known in this species especially when size differences are great and availability of food is limited (Rose, 1950). The behavior resulting in a nip was observed to be very similar or identical to that leading to consumption of liver. Only the size and movement of the other frog seemed to prevent the completion of the act of eating in the case of the nip. The increase in frequencies of nips, pushes and approaches in the presence of food is further evidence supporting this assumption. If the observations noted above are valid the attempt to obtain food may constitute a common basis for aggression in many vertebrates.

A short time after a unit of food is placed in an aquarium with a group of twelve frogs the frequency of sweeping motions with front feet and the amount of swimming activity both increase as do frequencies of all types of contacts. Even after food has been eaten the increased activity continues for 10 - 30 minutes. A searching type of behavior by one or two frogs in a group initiates the same sort of activity among the others even in the absence of food. Thus, activity in the group can be initiated by the behavior of one or two members, and this factor enhances the chances of locating food. Food also is found sooner by chance with more animals occupying a certain

volume of water, and in addition the greater amount of individual activity no doubt requires the use of more energy. Table 10 shows the comparative amounts of food eaten by frogs when isolated, when paired and when in a group of twelve. The total amount of food consumed by frogs varies directly with the number of animals placed together. Differences in total food consumption between the isolated and paired situations are not statistically significant, but when frogs are observed in groups of twelve the total consumption is significantly greater than in either of the other two situations. If increased food consumption is actually of positive value to the animal, this may be an example of cooperation or the Allee Effect (Odum, 1953).

The present work has indicated the existence of certain behavioral entities by the method of analysis. It has also attempted to relate these entities one to another and relate them to certain broader aspects of living things such as physiology, aggression, cooperation and hierarchial behavior. An attempt at controlled observation is used here to facilitate an understanding of behavior both in one species and as a general phenomenon of life. While one person has been studying the behavior of these frogs, the data as tabulated in a sense have reflected certain aspects of human behavior. On the whole, correlations are higher in Group II than they are in Group I, when rankings in the three aggressive categories and the unknown are compared to each other and to rankings in other factors. It could be that frogs in Groups I and II were behaviorally differant; on the other hand, as a result of continued work with the animals, the experimenter may have learned to fit certain aspects of behavior into categories with greater ease in the second group. Assuming the latter, this probably represents greater

accuracy in determining categories in Group II. However, there still is a source of danger in the method of analysis used in this study. Division of the behavioral whole into such increasingly apparent categories or entities might encourage an observer to ignore relationships between parts and the behavioral whole. The parts versus the whole dichotomy is one that science has faced from the start, because an important feature of the scientific method is the analysis of wholes into parts. Often dichotomies are eliminated as more is known about a subject. For instance, the study of heredity and environment has become not so much a problem of two separate things as different aspects of the same thing. Likewise, future work may show that heirarchial behavior is a special case of territoriality or vice versa.

Much of this work has centered around the study of individual differences in aggression, i. e. the determination of the presence of and form of hierarchial behavior in this frog. An analysis of hierarchial behavior is also attempted. An increasing number of studies in animal behavior are not concerned with an analysis of both the phenomenon of aggression and of the hierarchy (Allee, Foreman, Banks and Holabird, 1955; Braddock, 1949; Bovjberg, 1956; Crawford, 1940; Collias, 1943; Douglis, 1948; Greenberg, 1947; and Delany, 1955). Such studies represent attempts to analyze the broader aspects of behavior.

Many European workers, especially the ethologists, emphasize the analysis of more basic behavioral entities as is evident in the studies of releaser mechanisms (Tinbergen, 1942, 1948, 1953), social facilitation (Darling, 1938; Davies, 1953), displacement activities (Lorenz, 1941; Tinbergen, 1953) and imprinting (Lorenz, 1952).

The differences which exist between these two schools in their approaches to the general study of behavior are also evident in their approaches to the study of behavioral evolution. This is clearly shown when the European viewpoint discussed by Lorenz (1950) is compared with the American approach as indicated by Allee (1952). The Europeans attempt to compare more basic behavioral entities among different species whereas the Americans attempt a comparison of more general phenomena. Both approaches are of course useful in any study of evolution be it organic or behavioral.

## SUMMARY AND CONCLUSIONS

A study was made of two groups of twelve frogs in an attempt to analyze aggression and to determine whether individuals within the groups express aggressive differences resulting in hierarchial behavior.

1. Aggression in Xenopus laevis Daudin is displayed behaviorally in one of three ways, namely, by the approach, the push and the nip. These categories also represent increasing intensities of aggressive behavior in the order given.

2. Contacts representing the more intense categories of aggressive behavior occur less frequently than do those representing the less intense ones in both the paired and grouped situations.

3. Large differences among frogs are indicated when aggressive activity is totalled for each animal. Frogs displaying the most aggressive activity in one category tend to display the most in the others.

4. Differences in amount of aggressive behavior displayed between members of pairs are statistically significant in 50 per cent of the cases. This is consistent for each of the aggressive categories.

5. A category designated as unknown represents contacts in which no aggressive differences between animals could be determined. The total frequency of these kinds of contacts is as great as all other types combined.

6. Frogs with greater aggressive potentials, as measured by number of nips, pushes and approaches, experience fewer aggressive advances from other frogs and vice versa.

7. Heavier frogs display aggressive behavior more frequently than

lighter ones, yet are not necessarily the more active animals (activity referring to ranking in the unknown category).

8. The more aggressive as well as more active frogs eat more than the less aggressive and less active animals, yet when rankings in total food consumed are compared to rankings in total food consumed by others in their presence the results are not necessarily highly correlated.

9. No consistent relationships exist among rankings in food consumption, time taken to locate food while isolated and weight.

10. As the number of animals placed together is increased to twelve, the amount of food consumed by each frog increases. This may be an example of cooperation or the Allee Effect.

11. It is possible that aggressive behavior in these frogs reflects an attempt to eat one another, as behavior resulting in a nip is nearly identical to that which leads to consumption of liver.

## LITERATURE CITED


Allee, W. C., 1951. Cooperation among Animals, with Human Implications. Schuman, New York. 233 pp.

-----, 1952. Dominance and hierarchy in societies of vertebrates; cited in Structure et Physiology des Societes Animales, ed. Pierre Grasse, (Coll. Internat. Centre. Nat. Resh. Sci., 34: 157-181).

-----, and J. C. Dickinson, 1954. Dominance and subordination in the smooth dogfish, Mustelus canis (Mitchill). Physiol. Zool., 27(4):356-364.

-----, and M. Douglis, 1945. A dominance order in the hermit crab, Pagurus longicarpus Say. Ecology, 26:411-412.

-----, D. Foreman, E. M. Banks and C. H. Holabird, 1955. Effects of an androgen on dominance and subordinance in six common breeds of Gallus gallus. Physiol. Zool., 28(2): 89-115.

-----, B. Greenberg, G. M. Rosenthal and P. Frank, 1948. Some effects of social organization on growth in the green sunfish, Lepomis cyanellus. Jour. Exp. Zool., 108:1-19.

Banks, E. M., 1956. Social organization in red jungle fowl hens (Gallus gallus subsp.), Ecology, 37:239-248.

Bennett, M. A., 1939. The social hierarchy in ring doves. Ecology, 20(3): 337-357.

Bovjberg, R. V., 1953. Dominance order in the crayfish, Oronectes virilis Hagen. Physiol. Zool., 26:173-178.

-----, 1956. Some factors affecting aggressive behavior in crayfish. Physiol. Zool., 29:127-136.

Braddock, J. C., 1945. Some aspects of the dominance-subordination relationship in the fish, Platypoecilus maculatus. Physiol. Zool., 29:176-195.

-----, 1949. The effect of prior residence upon dominance in the fish, Platypoecilus maculatus. Physiol. Zool., 22:161-169.

Carpenter, C. R., 1942. Sexual behavior of free ranging Rhesus monkeys (Macaca mulatta). I. Specimens, procedures and behavioral characteristics of estrus. J. Comp. Psychol., 33:113-143.

Collias, N. E., 1943. Statistical analysis of factors which make for success in intitial encounters between hens. Am. Nat., 77:519-538.

-----, 1944. Aggressive behavior among vertebrate animals. Physiol. Zool., 17:83-123.

Crawford, M. P., 1940. The relation between social dominance and the menstrual cycle in female chimpanzees. J. Comp. Psychol., 30:483-513.

-----, 1942. Dominance and social behavior, for chimpanzees, in a non competative situation. J. Comp. Psychol., 33:267-277.

Darling, F. F., 1938. Bird Flocks and the Breeding Cycle. The University Press, Cambridge. 124 pp.

Daudin, F. M., 1803. Historie Naturelle des Rainettes, des Grenouilles et des Crapauds. Paris. p. 85.

Davies, J. L., 1953. Colony size and reproduction in the grey seal. Proc. Zool. Soc. London., 123(II):327-332.

Delaney, M. J., 1955. The evolution of aggressive behavior in vertebrate animals (Unpublished). Dept. of Zool., Glasgow, Scotland. (Now at Univ. of Southhampton, England).

Diebschlag, E., 1941. Psychological observations on the rank order in the domestic pigeon. From the Zool. Inst. of the Univ. of Marburg. (Psychologische beobachtungen uber die rangordnung bei der haustaube. Zeitschr. f. Tierpsychol., 4:(H.2) 173-188).

Douglis, M., 1946. Some evidence of a dominance-subordinance relationship among lobsters. Anat. Rec., 96:553. (Abstract).

-----, 1948. Social factors influencing the hierarchies of small flocks of domestic hen: The interaction between resident and part time members of organized flocks. Physiol. Zool., 21:147-182.

Edwards, A. L., 1954. Statistical Methods for the Behavioral Sciences. Rhinehart and Company, Inc., New York. 542 pp.

Elkan, E., and R. W. Murray, 1951. New laterial line sensory organs in Xenopus laevis. Nature, 168(4272:477.

Goin, Coleman J., 1953. Personal Communication.

Goin, Olive B., 1955. World Outside My Door. MacMillan Co., New York. p. 43.

Gordon, K., 1940. Territorial behavior and social dominance among Scuiridae. J. Mammal., 17:171-172.

Grant, W. C., 1955. Territorialism in two species of salamanders. Science, 121(3135):137.

Greenberg, B., 1947. Some relations between territory, social hierarchy and leadership in the green sunfish, Lepomis cyanellus. Physiol. Zool., 20:267-299.

-----, and G. K. Noble, 1944. Social behavior of the American chameleon, Anolis carolinensis Voigt. Physiol. Zool., 17:392-439.

Guhl, A. M., and W. C. Allee, 1944. Some measureable effects of social organization in flocks of hens. Physiol. Zool., 18:320-347.

Hammerstrom, F., 1942. Dominance in winter flocks of chickadees. Wilson Bull., 54:32-42.

Haskins, C. P., 1951. Of Societies and Men. Norton, New York. 282 pp.

Howard, W. E., and J. T. Emlen, Jr., 1942. Intercovey social relationships in the valley quail. Wilson Bull., 54:162-170.

Keith, A., 1949. A New Theory of Human Evolution. Philosophical Library, New York, 451 pp.

Leslie, J. M., 1890. Notes on the habits and oviposition of Xenopus laevis. Proc. Zool. Soc., London. 69-71.

Lorenz, K., 1941. Vergleichende bewegungsstudien an anatinen'. Jour. f. Ornithol., 89(Festschrift Heinroth):194-294.

-----, 1950. The comparative method in studying innate behavior patterns. Physiological Mechanisms in Animal Behavior. Academic Press, New York. 221-268.

-----, 1952. King Solomon's Ring. Thomas Y. Crowell Co., New York. 202 pp.

Lowe, M. E., 1956. Dominance-subordination relationships in the crawfish, Cambarellus shufeldtii. Tulane Studies in Zoology, 4(5):139-170.

Martof, B. S., 1953. Territoriality in the green frog, Rana clamitans. Ecology, 34:156-174.

Maslow, A. H., 1940. Dominance quality and social behavior in infra-human primates. J. Soc. Psychol., 11:313-324.

Munro, A. F., 1953. The ammonia and urea excretion of different species of amphibians during development and metamorphosis. Biochem. Jour., 54:29-36.

Newman, M. A., 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool., 29:64-81.

Odum, E. P., 1953. Fundamentals of Ecology. W. B. Saunders Co., Philadelphia. 384 pp.

Pardi, L., 1948. Dominance order in Polistes wasps. Physiol. Zool., 21:1-13.

Parker, F. Jr., S. L. Robins and A. Loveridge, 1947. Breeding, rearing and care of the South African clawed frog (Xenopus laevis). The Amer. Nat., 41:38-49.

Paterson, Nellie F., 1951. The nasal cavities of the toad Hemipipa carvalhoi Mir-rib and other Pipidae. Proc. Zool. Soc., London, 121(2):381-415.

Pearson, P. G., 1955. Population ecology of the spadefoot toad, Scaphiopus h. Holbrooki (Harlan). Ecological Monographs, 25:233-267.

Rose, W., 1950. The Reptiles and Amphibians of Southern Africa. Maskew Miller Ltd., Cape Town. pp. 1-34.

Sabine, W. S., 1949. Dominance in winter flocks of juncos and tree sparrows. Physiol. Zool., 22:64-85.

Schjelderup-Ebbe, T., 1913. Honsenes stemme fidrag til Honsenes psykologi naturen, 37:262-276.

-----, 1935. Social behavior of birds; cited in C. A. Murchinson, A Handbook of Social Psychology. Worchester. Pp. 947-972.

Sherif, M., 1956. Experiments in group conflict. Scientific American, 195(5):54-58.

Test, F. H., 1954. Social aggressiveness in an amphibian. Science, 120(3108):140.

Tinbergen, N., 1942. An objectivistic study of the innate behaviour of animals. Series D. Bibliothica Biotheoretica. V.1 pars 2. E. J. Brill, London. pp. 39-98.

-----, 1948. Social releasers and the experimental method required for their study. Wilson Bull., 60:6-52.

-----, 1953. Social Behaviour in Animals, with Special References to Vertebrates. Methuen and Co., Ltd., London. John Wiley and Sons, Inc., New York. 150 pp.

Uhrich, J., 1938. The social hierarchy in albino mice. Jour. Comp. Psychol., 25:273-413.

Walker, C., 1952. Clawed toad capital of America. The Sunday Sun Magazine Metrogravure. Baltimore, Md., April 30.

Yerkes, R. M., 1939. Social dominance and sexual status in the chimpanzee. The Quarterly Review of Biology, 14:115-136.

## BIOGRAPHICAL ITEMS

Robert Rice Haubrich was born in Claremont, New Hampshire, May 4, 1923 and graduated from Stevens High School, Claremont, in June, 1941. He entered the University of New Hampshire in the fall of 1941 and after three semesters entered the Army Air Force where he spent three years.

In March, 1946, he entered Michigan State University and received a Bachelor of Science degree in Forestry (1949) and a Master of Science degree in Zoology (1952) from that institution. The summer of 1952 was spent at Point Barrow, Alaska, with the Office of Naval Research. He began his doctoral program at the University of Florida in September, 1952 and spent the summers of 1953 and 1954 at the Marine Biological Laboratory, Woods Hole, Massachusetts. While at the University of Florida he taught biology laboratory and general biology (C-61, C-62) and also was Assistant Resident Advisor in one of the housing areas on campus.

Mr. Haubrich is a member of Xi Sigma Pi, Phi Sigma, Sigma Xi, The Association for the Study of Animal Behaviour and the Ecological Society of America.

This dissertation was prepared under the direction of the chairman of the candidate's supervisory committee and has been approved by all members of the committee. It was submitted to the Dean of the College of Arts and Sciences and to the Graduate Council and was approved as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August 10, 1957

C. F. Byers
Dean, College of Arts and Sciences

Dean, Graduate School

SUPERVISORY COMMITTEE:

E. Ruffin Jones
Chairman

Lewis Berner

James H. Gregg

Coleman J. Goin

Rolland H. Waters

Stan E. Wimberly